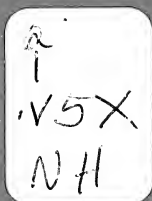


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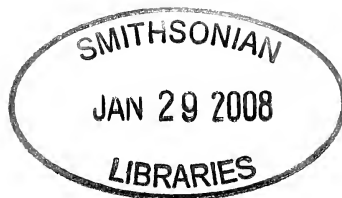
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Depauperate Small Mammal Communities in Managed Pine Plantations in Eastern Virginia

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ABSTRACT

Loblolly pine (*Pinus taeda* L.) plantations of four different ages were examined to identify changes in the small mammal community in relation to changes in the vegetational community. Small mammals were evaluated during five seasons using two methods of trapping. Live traps accounted for 65% of captures and seven of nine species, whereas pitfall traps yielded eight species, of which two were not taken with live traps. For both trap types, catch rates averaged less than two per 100 trap-nights, very low even for pine forests. Both abundance and biomass of small mammals declined with increasing stand age, whereas species diversity increased with increasing stand age. The relative proportions of trophic groups changed after crown closure from mostly granivores and omnivores to mostly insectivores. However, after mechanical thinning of late-age stands, small mammals of forested habitats and of early successional habitats were found together. The numbers of trapped small mammals decreased progressively throughout the study. We speculate that weather events might have contributed to this pattern but the reasons are unknown.

INTRODUCTION

Small mammals of forests often show preferences for habitats differing in age and structure (Linzey and Linzey 1973, Kirkland and Griffin 1974, Dueser and Shugart 1978). Thus, the abundance and species of small mammals inhabiting recent clearcuts often differ greatly from those found in maturing forests. Furthermore, secondary succession sometimes is governed by attributes of the initial disturbance (Boring et al. 1981). For example, timber management practices such as site preparation and the use of herbicides, pesticides, fertilizers, and selective cutting can directly affect the composition of the plant community, and in turn indirectly affect small mammal communities.

Much research has evaluated changes in small mammal communities in relation

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to vegetation changes in hardwood forest systems in eastern North America (e.g., Kirkland 1977, McComb and Rumsey 1982, Martell 1983, Buckner and Shure 1985). However, fewer studies have been conducted on small mammals in pine plantations in the Southeast. Atkeson and Johnson (1979) and Mengak et al. (1989) studied small mammals in pine plantations in the piedmont regions of Georgia and South Carolina, respectively, and Mitchell et al. (1995) studied small mammals in pine plantations on cleared pocosins in coastal North Carolina. In contrast, our study examined small mammal communities in managed loblolly pine plantations on upland sites in the coastal plain of Virginia, a region in which commercial stands of such pines often locally comprise a majority of the forested landscapes.

To learn details of changes in the small mammal community in relation to age of pine stand, we chose pine plantations of ages 1, 8, 18, and 24 years. In eastern Virginia, most loblolly pine (*Pinus taeda* L.) plantations are harvested at ca. 30 years of age. Our objectives were to determine the relative abundance, biomass, and species diversity of small mammal communities in relation to the age of managed pine plantations, to examine seasonal changes in the small mammal communities of these stands, and to document the presence or disappearance of small mammal species with age of pine stand.

MATERIALS AND METHODS

Study sites, selected from holdings of The Union Camp Corporation, were located in Isle of Wight County, in the Southeastern Coastal Plain Region of Virginia. Pine trees had been planted at densities of 1042-1482 stems/ha using mechanical planters after stumps and debris had been pushed into windrows. We chose four age classes of pine plantations on sites in relatively close proximity (1-16 km apart) to minimize the effects of variation in local weather conditions. We had no control over the herbicide, pesticide, or thinning treatments applied to some forest stands; we sought replicate sites that were as similar as possible. We had three replicates of the 1- and 24-year-old stands, and two replicates of the 8- and 18-year-old stands.

We trapped during five seasonal periods: (1) 12 June - 26 July 1995, (2) 20 October - 3 December 1995, (3) 19 January - 3 March 1996, (4) 3 April - 17 May 1996, (5) 9 July - 22 August 1996. The interval between seasons was at least 30 days.

Small Mammal Trapping

Effective surveys of small mammals require two methods of trapping, one of them being removal trapping (e.g., Getz 1961; Wiener and Smith 1972). Because pine forests support low-density populations of most small mammal species (Mengak et al. 1989, Mitchell et al. 1995) and removal trapping can locally reduce population density, we chose to use four 0.25 ha grids separated from one another by at least 50 m rather than one large hectare grid at each site. This design produces twice as much edge as one large grid, enabling small mammals living on the margins to enter the 0.25 ha grids after pitfall trapping had reduced abundances within the grids, potentially allowing populations to recover quickly.

The 50 m X 50 m (0.25 ha) grids were established at each site, each with 25 trap stations 12.5 m apart. A minimum buffer zone of 50 m separated grids from both the edge of a site and from one another. One Fitch live trap (Rose 1994) and one # 10 can

pitfall trap were placed within 1 m of each grid coordinate. (Fitch traps are superior to Sherman traps in capturing two common rodents in this study, white-footed mice and hispid cotton rats (Rose et al., 1977)). Live traps were baited with birdseed, tended for nine consecutive days, followed by at least seven days of no trapping, and finally by seven consecutive days of pitfall trapping. All traps were checked daily. Pitfall traps were buried to ground level and ca. 5 cm of water was placed in each trap. Pitfall traps were turned over and thereby made non-functional, except during active pitfall trapping. When captured, each animal was identified, weighed, and painted with permanent marker so that it was counted only once for that season.

Assessment of Vegetation

All planting rates are from information provided by Union Camp personnel. Vegetation data were recorded in late spring 1996, thus allowing one-year-old pine stands to go through two complete growing seasons to give more meaningful assessments of the early plant community. We estimated the percent of ground-level vegetation cover using a 0.3-m² frame placed flat on the ground (modified from Brower et al. 1990). Heights (m) of pines and of understory shrubs and trees were assessed by using a reference pole (James and Shugart 1970). Leaf-litter depth was measured using a 10-cm rod marked at 1-cm intervals and coarse woody debris was classified into four categories: none, scattered, moderate, and extensive. Ten randomly selected pine trees in each grid were measured for diameter at breast height (dbh).

Analysis of the Small Mammal Community

Small mammal communities were characterized using five indices: success by type of trap, presence or absence, total captures, biomass, and species diversity (Shannon-Wiener Index (H')). The total number of captured individuals per species serves as a measure of relative abundance for each species (Mitchell et al. 1995). Biomass was determined by summing the masses of all individuals trapped during each season. Differences in total individuals, biomass, species diversity, and means of trap success were evaluated using a Model I, 1-Factor ANOVA at an alpha level of 0.05; trends in species distribution, total captures, and biomass were analyzed using a Runs Up-and-Down test (t_s); and bivariate correlations were determined for small mammal community indices and stand age using the Pearson's correlation coefficient (Sokal and Rohlf 1995).

RESULTS

Descriptions of Pine Stands

One-year-old stands had grass coverage that varied widely (0-100%) among grids and pine saplings averaging 2.5 m. Planting rates averaged 1359 stems/ha. Density of woody debris varied from none to moderate amounts. The understory, comprised primarily of blackberry (*Rubus allegheniensis* Porter), poison ivy (*Toxicodendron radicans* (L.) Kuntze), wild grape (*Vitis* spp.), dogfennel (*Eupatorium capillifolium* (Lamarck) Small), yellow jessamine (*Gelsemium sempervirens* St. Hilaire), broomsedge (*Andropogon virginicus* L.) and panic grass (*Panicum* spp.), was moderately open and included volunteer hardwood species (mostly sweet gum (*Liquidambar styraciflua* L.) and red maple (*Acer rubrum* L.) saplings).

Eight-year-old stands had complete crown closure, were devoid of grasses, had a 3.5 cm litter layer, and no woody debris. Pines averaged 9 m with a dbh of 15 cm and had a 90 % survival rate. Original planting rates averaged 1235 stems/ha. Volunteer hardwood trees were found primarily along the windrows of debris from previous logging activities. The understory, open below 0.5 m and moderately dense from 0.5-3.0 m, was comprised of highbush blueberry (*Vaccinium corymbosum* L.), sweet-pepperbush (*Clethra alnifolia* L.), wild grape, greenbrier (*Smilax rotundifolia* L.), Japanese honeysuckle (*Lonicera japonica* Thunberg), blackberry, poison ivy, and American cane (*Arundinaria gigantea* (Walter)).

Eighteen-year-old stands had little or no woody debris, no grasses, and a 3.7 cm litter layer. Pines averaged 12.5 m with an average dbh of 18.5 cm and had 91% survival for 1235 stems/ha. Understory plants, similar to those of 8-year-old stands, were dense from 0-2 m and moderately dense from 2-3 m.

The two unthinned 24-year-old stands averaged of 579 pine and 372 hardwood stems/ha. Litter averaged 4.6 cm deep; moderate amounts of woody debris but no grasses were present. Pines averaged 14 m and 26.75 cm dbh. The understory remained similar but American cane was now dominant.

The 24-year-old thinned stand had elements of both early and late vegetation communities. Before thinning, there were 1110 pine and 85 hardwood stems/ha. When trees were removed from every fifth row, an understory dense up to 1 m and similar in composition to that of 1-year-old stands was created. Unthinned rows remained devoid of grasses with moderate amounts of woody debris and a 2.2 cm deep litter layer. Pines averaged 16 m and 23.5 cm in dbh. The understory, moderately dense from 0.5-3 m, was composed primarily of highbush blueberry and sweet-pepperbush.

Trapping of Small Mammals

In 67,950 trap-nights, 1,039 small mammals of nine species were captured (Table 1). This represents an overall catch rate of 1.53 small mammals per 100 trap-nights (one trap in place for one night equals one trap-night) for both trap types. In 39,600 trap-nights, 672 small mammals of seven species were captured in live traps, for a capture rate of 1.7 per 100 trap-nights, whereas during 28,350 nights of pitfall trapping, 367 small mammals representing eight species were captured (1.29 mammals/100 trap-nights). The capture rates per 100 trap-nights of both trap types combined declined progressively across the five seasons from 2.8, 2.0, 1.7, 1.2, to 0.6, respectively.

Our assessment of the composition of the small mammal community was influenced by trap type (Table 1). Least shrews (*Cryptotis parva* Pomel) and southeastern shrews (*Sorex longirostris* Bachman) were taken only in pitfall traps, whereas hispid cotton rats (*Sigmodon hispidus* Say and Ord) were captured exclusively in live traps. All other species were captured in both trap types, but with varied capture rates.

The Community of Small Mammals

The proportions of different shrew species were relatively constant in pine stands of different ages (Table 2). Short-tailed shrews (*Blarina brevicauda* Gray), significantly more numerous in 18-year-old stands than in other stands ($F = 39.97$, $P < 0.001$), were significantly more numerous than least shrews there ($F = 11.98$, $P =$

TABLE 1. Totals and percent of small mammals captured by trap type across all seasons and ages of pine stands combined.

Small Mammal Species	Total	% by live traps	% by pitfall traps
Short-tailed shrew			
<i>Blarina brevicauda</i>	73	56	44
Least shrew			
<i>Cryptotis parva</i>	38	0	100
Southeastern shrew			
<i>Sorex longirostris</i>	212	0	100
Pine vole			
<i>Microtus pinetorum</i>	61	66	34
House mouse			
<i>Mus musculus</i>	36	72	28
Eastern harvest mouse			
<i>Reithrodontomys humulis</i>	26	73	27
White-footed mouse			
<i>Peromyscus leucopus</i>	378	91	9
Golden mouse			
<i>Ochrotomys nuttalli</i>	130	91	9
Hispid cotton rat			
<i>Sigmodon hispidus</i>	85	100	0

0.037). Least shrews maintained relatively constant numbers in all stand ages. Southeastern shrews, captured in all but one stand, had significantly higher numbers than other shrews in the 24-year-old stands ($F = 7.02$, $P = 0.027$). The southeastern shrew also had a significantly higher abundance than the least shrew in 18-year-old stands ($F = 12.04$, $P = 0.037$). Despite these significant differences, mean numbers of shrews in each stand across the five seasons were small, usually <5 but sometimes as high as 12 and 13 per season.

Unlike shrews, the abundance of most rodent species varied considerably among pine stands of different ages (Table 2). Exceptions to this pattern were pine voles (*Microtus pinetorum* (LeConte)) and house mice (*Mus musculus* L.), which, except that the latter was absent in 18-year-old stands, had similar but low mean abundances in all stands. Eastern harvest mice (*Reithrodontomys humulis* (Audubon and Bachman)) were present only in 1- and 24-year-old stands. By contrast, white-footed mice (*Peromyscus leucopus* (Rafinesque)) dominated and had significantly higher numbers in the 1-year-old stands than in other age classes ($F = 19.62$, $P < 0.001$). White-footed mice were absent from both 8-year-old stands and one of the two 18-year-old stands; they reappeared in low numbers in 24-year-old stands.

By contrast, golden mice (*Ochrotomys nuttalli* (Harlan)) were captured in all except 1-year-old stands (Table 2). The golden mouse was significantly more abundant

Table 2. Mean numbers of animals (averaged across seasons, rounded to the nearest whole number) of small mammals in pine stands of ages 1, 8, 18, and 24 years. Grand means (\bar{x}) are for the same age classes combined, given to one decimal place. The asterisks (*) denote sites treated with herbicides and insecticides by the Union Camp Corporation. Common names are defined in the legend to Table 1.

Species	Pine Stand Age											
	1	1*	1*	\bar{x}	8	8	8	\bar{x}	18	18	24	\bar{x}
Short-tailed shrew	1	1	1	1.0	1	1	1	1.0	3	4	1	1.0
Least shrew	7	0	0	2.3	1	1	1	1.0	1	0	1	1.0
Southeastern shrew	13	1	0	4.6	12	1	1	6.5	4	3	2	3.3
Pine vole	3	0	1	1.3	1	0	0	0.5	1	2	1	1.3
House mouse	1	4	4	3.0	2	0	0	1.0	0	0	0	0.3
Eastern harvest mouse	1	3	2	2.0	0	0	0	0.0	0	0	1	0.7
White-footed mouse	18	32	22	24.0	0	0	0	0.0	1	0	4	4.6
Golden mouse	0	0	0	0.0	7	5	5	6.0	5	4	2	2.7
Hispid cotton rat	10	5	2	5.6	1	1	1	1.0	0	0	0	1.0

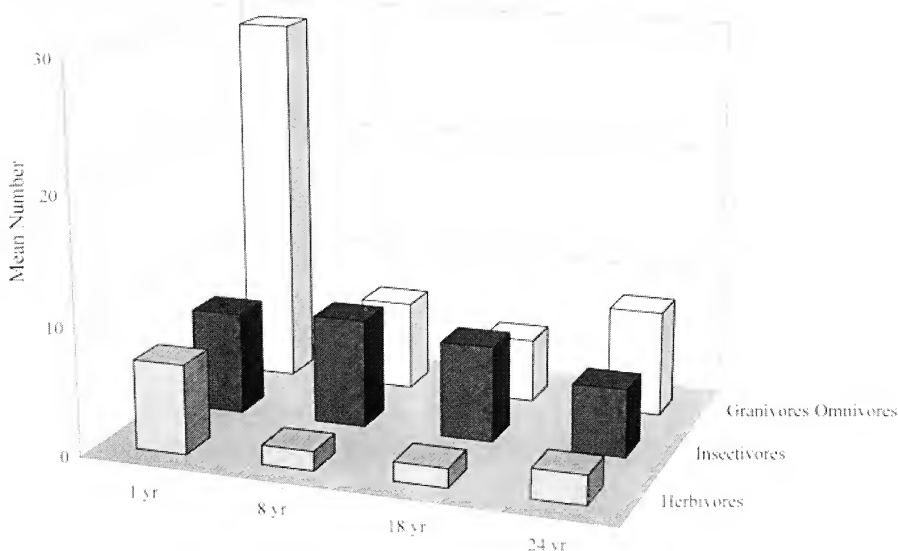


FIGURE 1. Mean numbers of small mammals collected during the study in pine stands of four ages, based on the trophic group to which they belonged (similar to the expanded data in Table 3).

in 8- and 18-year-old pine stands than in other age classes ($F=8.91$, $P=0.013$) and was significantly more abundant than other rodents in 8-year-old ($F=13.98$, $P=0.003$) and 18-year-old stands ($F=25.13$, $P<0.001$). The hispid cotton rat usually was captured in low numbers but it was absent in 18-year-old stands.

Trophic groups of small mammals

The proportions of trophic groups differed somewhat among age classes of pine stand (Table 3). Insectivores made up a significantly higher proportion of totals in the 18-year-old stands than other trophic groups ($F=23.22$, $P=0.015$). Granivores/omnivores (*Mus*, *Reithrodontomys*, *Peromyscus*, *Ochrotomys*) comprised a significantly higher proportion of small mammals than other trophic groups (Figure 1) in both 1-year-old ($F=8.56$, $P=0.018$) and 24-year-old stands ($F=38.15$, $P<0.001$).

No significant trends were found in herbivores (*Microtus* and *Sigmodon*).
Abundances, biomasses, and diversity.

Despite using four 0.25-ha grids instead of one 1-ha grid in each stand (thus promoting the possibility of immigration from adjacent habitat onto each small grid), mean abundances for all sites declined progressively with each season (45, 27, 22, 16, 8 animals; not shown because these results are not directly relevant to composition changes of the small mammal community in relation to age of pine stands). All stands had declining capture trends over successive trapping seasons ($t_s=3.74$, $P\leq 0.05$).

TABLE 3. Mean numbers of animals and percent of catch of trophic groups of small mammals for all seasons combined in pine stands of ages 1, 8, 18, and 24 years. Grand means (\bar{x}) are for same age classes combined, given to one decimal place. Insectivores include all three shrews, granivores/omnivores are defined as house, eastern harvest, white-footed, and golden mice, and herbivores are pine voles and hispid cotton rats. The asterisks (*) denote sites treated with herbicides and insecticides by the Union Camp Corporation.

Trophic Groups	Pine Stand Age											
	1	1*	1*	\bar{x}	8	8	\bar{x}	18	18	\bar{x}	24	\bar{x}
Insectivores												
Means	21	2	1	8.0	14	3	8.5	8	7	7.5	4	5.3
Percent	39	4	3	18.2	56	33	50.0	54	54	53.6	33	33.3
Granivores/Omnivores												
Means	20	39	28	29.0	9	5	7.0	6	4	5.0	6	8.3
Percent	37	85	88	65.9	36	56	41.2	40	31	35.7	50	52.1
Herbivores												
Means	13	5	3	7.0	2	1	1.5	1	2	1.5	2	2.3
Percent	24	11	9	15.9	8	11	8.8	7	15	10.7	17	14.6

The number of live-trapped small mammals ($n = 268$) was much higher in summer 1995 than in summer 1996 ($n = 78$), contributing to the significant differences in abundances among seasons ($F = 3.40$, $p = 0.018$).

Significantly higher abundances were observed in 1-year-old stands than in other stands ($F = 6.49$, $P = 0.001$; Table 4). A significant negative correlation was found for the number of captures with stand age ($r = -0.517$, $P < 0.001$).

Biomass of small mammals followed a pattern similar to number of captures (Table 4), namely it was significantly higher in 1-year-old stands than in other stands ($F = 6.49$, $P = 0.001$). A significant negative correlation was found for small mammal biomass with stand age ($r = -0.481$, $P = 0.001$).

Unlike abundance, the biomass differences between consecutive trapping seasons were not significant. However, as with number of captures, all stands had declining biomass trends over successive trapping seasons ($t_s = 4.09$, $P = \leq 0.05$). Mean biomass declined progressively with each successive season (832, 677, 366, 216, 104 g).

Finally, differences in average species diversity of small mammals among age classes of pine stands (Table 4), as measured by the Shannon–Wiener index (H'), were not significant. However, a significant positive correlation was found between species diversity and stand age ($r = 0.353$, $P = 0.019$).

DISCUSSION

More small mammals were caught per 100 trap-nights for live traps (1.70) than per 100 pitfall trap-nights (1.29). These are very low catch rates for small mammals in forests (see beyond), especially for live traps. Live traps were more successful than pitfalls at catching granivores/omnivores and herbivores, probably due to the attraction of bait and the ability of some small mammals, such as adult hispid cotton rats, to escape from pitfall traps. Pitfall traps accounted for only 12% of all rodent captures (Table 1). However, pitfall traps were more effective than live traps at catching shrews, accounting for 87% of shrew captures (Table 1). Shrews are primarily insectivorous and therefore less attracted to baits used in live traps. Many investigators (e.g., Hudson and Solf 1959, Brown 1967, Briese and Smith 1974, Williams and Braun 1983) have also found pitfall traps to be more effective than live traps for capturing shrews.

Live traps failed to catch least shrews and southeastern shrews, and pitfall traps caught no cotton rats. Thus, two (or more) trap types are necessary to obtain the most accurate depiction of a small mammal community (Getz 1961, Wiener and Smith 1972).

Shrew Abundance and Distribution

Although the composition of the shrew community remained relatively constant in the four age stands (Table 2), shrew abundances varied somewhat among pine stands of the same age. Such variation is probably due to local site differences. Similar to Mengak et al. (1989), short-tailed shrews had greatest abundances in 18-year-old stands, likely due to the high density of American cane on those sites. However, these greater abundances may not be directly related to the American cane, but, as Getz (1961) suggests, to a response to the soil moisture conditions in which the American cane thrives.

By contrast, the southeastern shrew was uniformly most numerous, varying among

TABLE 4. Means of community parameters of small mammals found in four ages of pine stands for all seasons combined. Grand means (\bar{x}) are for all same-age classes combined. The asterisks (*) denote sites treated with herbicides and insecticides by the Union Camp Corporation.

Community parameter	Pine Stand Age											
	1	1*	1*	\bar{x}	8	8	8	\bar{x}	18	18	18	\bar{x}
Abundance (no.)	54	46	32	43.8	25	9	17	15	13	12	15	15.9
Biomass (g)	1105	824	760	896	236	212	224	181	180	216	197	276
Species Diversity (H')	1.04	0.55	0.64	0.74	0.85	0.94	0.89	0.95	0.81	1.13	1.31	1.19

means of 3.3-6.5 per site (Table 2). The ability of the southeastern shrew to flourish in all stand ages is due in part to its ability to tolerate low soil moisture. Using pitfall traps on similar 0.25-ha grids, Rose et al. (1990) found southeastern shrews at dozens of locations in southeastern Virginia, ranging from boggy sites with peaty soils to those with dry mineral soils.

Rodent Abundance and Distribution

The rodent community varied among age classes of pine stand (Table 2), a response to the changing plant community (Atkeson and Johnson 1979, Mengak et al. 1989). Cotton rats, harvest mice, and house mice prefer oldfield habitats having a substantial amount of vegetative cover (Atkeson and Johnson 1979), such as was found in 1-year-old stands. Absent after crown closure, these rodent species reappeared in the 24-year-old stands, but at lower abundances (Table 2), associated with the reappearance of grasses and forbs in the more open thinned stand. Unlike other rodents, the semi-fossorial pine vole was found in all stand ages at relatively constant low abundances (Table 2).

Mengak and Guynn (2003), who also studied small mammals in loblolly pine forests, used discriminant function analysis to relate capture rates to habitat variables for the six species sufficiently numerous to merit analysis. In part because they used only snap traps, they caught too few least or southeastern shrews, house mice, or pine voles to include in their analyses. Nevertheless, some comparisons with our study are possible, such as the virtual disappearance of harvest mice and cotton rats by 8 years, the mutual patterns of abundance of these two species, and the importance of dense covering vegetation near ground level for both species. Other investigators, especially Cameron and his colleagues (Joule and Cameron 1975, Cameron 1977, Cameron et al. 1979), have published on this *Sigmodon-Reithrodontomys* association.

White-footed mice were numerically dominant only in the 1-year-old stands (Table 2), and although virtually absent in 8- and 18-year-old stands, more were captured in 24-year-old stands. Our results are similar to Atkeson and Johnson (1979), who found white-footed mice in greatest abundances in 1-year-old pine stands and decreasing with stand age thereafter. Its presence in 24-year-old stands is not surprising because white-footed mice are considered to be arboreal and well adapted to life in forests (Shure 1970, M'Closkey and Fieldwick 1975, Dueser and Shugart 1978, Kantak 1983, Rose and Walke 1988). However, as seen in our study, the white-footed mouse also is an excellent colonizer of early seral stages and usually rapidly increases in abundance immediately after clearcutting (Gashwiler 1959, Verme and Ozoga 1981).

Unlike other rodents, golden mice were found in all except 1-year-old stands (Table 2). Golden mouse numbers were highest in 8-year-old and 18-year-old stands, probably due to the presence of the dense intertwined understory they prefer and perhaps to the virtual absence of their close relative and potential competitor, the white-footed mouse, in these stands. The arboreal golden mouse is a habitat specialist, selecting habitats with an understory of vines and bushes (Barbour 1942, Goodpaster and Hoffmeister 1954, Linzey and Packard 1977). Atkeson and Johnson (1979) found peak abundances of golden mice at stand age 7, results similar to ours. Knuth and Barrett (1984) report that golden mice compensate for their habitats having low quality and widely dispersed food sources by having lower body temperatures and metabolic rates but higher assimilation

efficiencies than similar small rodents, such as white-footed mice.

Although both species were captured in the same 24-year-old stands, white-footed and golden mice were not captured in the same microhabitats (personal observation). Golden mice were captured most frequently in dense microhabitats, whereas white-footed mice were captured most often in more open microhabitats. Seagle (1985) suggests that competition between golden and white-footed mice is reduced by selection of different microhabitats and that disturbances such as thinning create a mosaic of microhabitats, thereby facilitating their coexistence.

Trophic Groups

Our finding that insectivores comprised a large proportion of small mammals in 8- and 18-year-old stands probably was due to the low numbers of rodents there. Because numbers of insectivores remained relatively constant in the stands of different age (5.3-8.5; Table 3), proportions were influenced more by abundances of other trophic groups than by changes in insectivore abundance. Mengak et al. (1989) report similar results for 18-year-old pine stands. Presence and abundance of insectivores may depend more on prey populations of invertebrates and the related soil moisture than on the nature and quality of plant communities. However, in some instances, the proportions of trophic groups differed more within same-age stands than among stands of different ages (Table 3). This was most apparent in 1-year-old stands, where differences likely were due to the use of insecticides, which probably reduced the invertebrate prey base of insectivores on the two treated sites.

The high abundances of granivores/omnivores in 1- and 24-year-old stands (Table 3) likely were due to suitable habitat to support large populations of seed plants, herbaceous vegetation, and their associated organisms. Kirkland (1977) also found granivore/omnivore abundances to be highest in recent clearcuts. The moderate abundances of granivores/omnivores in 8- and 18-year-old stands were due primarily to presence of golden-mice (Table 3).

Herbivore numbers were uniformly the lowest of all trophic groups and remained relatively constant across age classes, although herbivores were somewhat more numerous in 1-year-old stands, similar to Atkeson and Johnson (1979). Interestingly, no meadow voles (*Microtus pennsylvanicus* (Ord)) were collected in our study. Before the movement from the south of cotton rats into Virginia (Patton 1941), meadow voles were the largest and most abundant herbivorous rodents in oldfield habitats in eastern Virginia (Handley and Patton, 1947).

Small Mammal Abundance

Small mammal abundances were highest in young stands and declined with increasing stand age (Table 4), reflecting the significant negative correlation between number of animals and age of stand. Large numbers of small mammals in young stands are the result of diverse plant communities (Boring et al. 1981) that are high in ground cover, grass cover, weedy annuals, and perennials (Mengak et al. 1989), thus providing sufficient food and cover for many kinds of small mammals (McComb 1982). As pines grow, the associated plant community becomes more homogenous and nearly devoid of grasses and forbs, thus supporting fewer and often different kinds of small mammals

than younger plant communities (McComb 1982). McComb and Rumsey (1982) report clearcuts with 1.5 times more small mammals than uncut sites. Even with pesticide and herbicide treatments, our 1-year-old stands had 2-3 times more small mammals than maturing stands.

Unlike Mengak et al. (1989), we observed no increases in small mammal numbers during the breeding seasons of spring and autumn, only a progressive decline. This systematic decline over successive trapping seasons has not been noted in previous studies, either in pine plantations or in other types of forest communities. The observed systematic decline in small mammal abundances in our study, seen in all stands, likely was caused by two factors that would have had relatively equal effects in all stands: removal trapping (and low immigration rates of animals from nearby onto depopulated grids) and weather.

Stickel (1946), Getz (1961), Smith et al. (1974), Kirkland (1977), Atkeson and Johnson (1979), Mengak et al. (1989), and many others have conducted removal trapping on small plots without finding the same declining trend in numbers as we did. In fact, it has been suggested that it is nearly impossible to deplete a small mammal community with seasonal removal trapping due to the rapid immigration of animals into unoccupied habitat. Recently, Sullivan et al. (2003) reported significantly higher small mammal numbers in removal sites (due to rapid colonization) than in control sites. Therefore, we believe that removal trapping did not cause the systematic decline of captures through the five seasons in our study.

Instead we implicate climatological factors that affected three of five seasons. Extreme environmental conditions sometimes increase mortality rates of small mammals and their effects can continue through the following breeding season. In July 1995, temperatures averaged 5.6 °C above normal with 19 of 31 days having high temperatures above 32.2 °C (NOAA, 1995), and precipitation was 8.21 cm below normal, creating drought-like conditions.

During January 1996, temperatures averaged 14.4 °C below normal with 24 of 31 days having low temperatures of below 0 °C (NOAA, 1996). Precipitation was 5.4 cm above normal with 27.7 cm of ground-covering precipitation in the form of snow or ice. In January and February 1996, three significant ice storms had potentially detrimental effects on the biota. During extreme winter conditions, some species of small mammals (e.g., *Sigmodon hispidus*) can go through local extinctions (Slade et al. 1984, Sauer 1985). Schmidt-Holmes and Drickamer (2001) also speculate that unusually cold temperatures caused high winter mortality, thereby depressing usual densities in the next breeding season.

Finally, the second summer, temperatures averaged only 1.4 °C below normal, but the 29.5 cm above normal precipitation created flooding in most stands. As with the other two periods of extreme weather conditions, it is likely that reproduction failed or was reduced. Thus, we believe that the effects of drought, unusually cold winter conditions, and flooding may be primarily or partially to blame for the progressively declining numbers of small mammals across our study.

Biomass

Strongly related to number and body size, biomass peaked in young pine stands and

decreased with stand age (Table 4), as has been found by many others (e.g., Atkeson and Johnson 1979; Mengak et al. 1989). This finding is not surprising because the young plant community is diverse and supports numerous and often large-bodied small mammals, resulting in high biomass. Not proportional to declines in abundance, much of the biomass decline was due to the presence or absence of the cotton rat, a species 5-30 times larger than the other small mammals in this community.

Species Diversity (Shannon-Wiener Index)

Species diversity increased with increasing stand age (Table 4). The high diversity in the 24-year-old stands may be partially due to the moderately heterogeneous plant communities of mixed pine and volunteer hardwood trees and areas of early successional habitat created by thinning. Although species diversity was highest there, all species were low in abundance. Our findings differed from those of Atkeson and Johnson (1979), who found species diversity to increase after clear-cutting and to attain highest values in stands of ages 1-4 years.

Pine Forests and Small Mammals

The moderately high diversity of the small mammal community of older pine plantations gives a false impression of quality. Overall, pine plantations support relatively low numbers of small mammals compared to other plant communities in eastern North America. Whether judged by live traps or pitfall traps, our catch rate averaged < 2 animals per 100 trap-nights across the study. Trap successes of 19 - 42% have been published for studies conducted in early successional (oldfield) habitats (McComb and Rumsey 1982, Buckner and Shure 1985, Healy and Brooks 1988), whereas somewhat lower trap successes (8 - 32%) are reported for hardwood and mixed forests (Kirkland and Griffin 1974, Healy and Brooks 1988, DeGraaf et al. 1991). The lowest trap successes, of 1 - 5% (our study, Mengak and Guynn 1987, Mengak et al. 1989, Mengak and Guynn 2003), were in pine plantations.

Although pine plantations live up to their nickname of "biological deserts," some timber management practices can create more suitable habitat for small mammals. For example, thinning every fifth row in 24-year-stands increased diversity of small mammals by creating favorable habitats as well as improving timber production. Windrows also enhance habitat quality for small mammals and other wildlife too.

Finally, although small mammals have no commercial value, they are important as the prey base for populations of many avian and mammalian wildlife, and probably in less well-studied subtle roles of soil mixing, distribution of important hypogeous fungi, consumption of insects, and dispersal of seeds. An understanding of how small mammals respond to different stages in pine growth can help forest managers and wildlife biologists manage pine plantations for mutual benefit, and by doing so, contribute to the conservation of biodiversity, as endorsed by the American Forest and Paper Association (2002).

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Efficiency of Mechanical Harvest for Immature Vegetable Soybean Pods¹

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ABSTRACT

Since soybean (*Glycine max* [L.] Merr.) is low in saturated fat and active in reducing blood cholesterol, it is gaining interest as a healthy snack food. Direct consumption of vegetable soybeans is very popular in the Orient. However, the cultivars used in Asia are not adapted to U.S. production systems. The objectives of this study were to determine the efficiency of mechanical harvest and to identify vegetable soybean cultivars adapted for a mechanical harvest system. To implement the objectives, four vegetable soybean cultivars were planted in a randomized complete block design at Randolph Research Farm, Virginia State University. The cultivars were hand harvested and mechanically harvested at the green pod stage and evaluated for green pod yield (kg ha⁻¹), one hundred pod weight (g), plant height (cm), and pod dimensions of length (cm), width (cm), and thickness (cm). A significant difference ($P < 0.01$) was observed among the two methods of harvesting. The hand harvested beans yielded twice as many more pods as the mechanical harvested beans. However, the pods harvested mechanically were cleaner and required no further cleaning as compared to hand harvested pods. There was also significant cultivar x method harvest interaction. The common bean picker was effective in harvesting the vegetable soybean cultivars with plant height of 55 to 66 cm and pod size that ranged from 128 to 144 g 100⁻¹ pods. This type of operation could be easily adapted by farmers using appropriate cultivars.

Key words: Vegetable soybean, cultivars, harvesting, mechanical, weight, yield, edamame

INTRODUCTION

In the United States (U.S.), an interest in healthier food is a driving force in the search for nutritious alternative crops. A quarter of the U.S. population has elevated cholesterol levels, a condition associated with a high risk of heart disease (Roberts, 1987). Many Americans are interested in consuming foods that lower blood cholesterol

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level. Among alternative vegetable crops, soybean has the distinction of being low in saturated fat and active in reducing blood cholesterol level. In addition, the Food and Drug Administration (1999) has approved the claim for the cholesterol lowering effect of soybean (*Glycine max* [L.] Merr.). Health benefits associated with soybean consumption include a cholesterol-free source of protein and lower intake of saturated fat. Several studies have shown a relationship between soy food consumption and the prevention of heart disease and cancer (Carroll and Kurowska, 1995; Kritchevsky, 1994; Potter, 1994). The announcement by FDA that soybean could lower the risk of heart disease further spurred the demand for frozen vegetable soybean. Educating the consumers with preparation, cooking, and consumption methods, and developing better flavor and quality varieties are very important for a dramatic increase in demand. The aging baby boomer generation is concerned with longevity and the prevention of chronic diseases. As a result, they seek functional foods such as soybeans including vegetable soybeans for healthy benefits.

Vegetable soybean or edamame is one potential crop that can bring economic benefits to the farmers. What makes vegetable soybean a new phenomenon is the snack itself, and the broader acceptance as an ingredient in cooking. Like all soybeans, vegetable soybeans are versatile: they can be served as a fresh cooked vegetable, included in salads, and roasted (Mebratu et al., 2005a, b). Generally, vegetable soybean is a large seeded variety harvested when the pods are fully filled but still green (Shanmugasundaram et al., 1991; Mebratu et al., 2005a,b). Vegetable soybean has a sweet and delicious taste, and can be eaten as a snack either boiled in water or roasted (Liu, 1999). The fresh beans can also be mixed into salads, stir-fried, or combined with mixed vegetables. Vegetable soybean is also used to make tofu, ice cream, and similar desert items (Shanmugasundaram et al., 1997).

Vegetable soybean is a new crop for most Virginia farmers and mechanical harvesting is essential to make edamame a profitable and manageable crop for large scale production. Silbernagel et al. (1991) reported that machine-harvest of common beans requires a uniform maturation where the majority of the pods are ready at the same time for once-over destructive harvest. Moreover, the best machine-harvested cultivars bear the pods in the mid to upper part of a sturdy upright plant. This allows for the highest pod yields.

There are three major constraints to large-scale vegetable soybean production in the U.S. First there is a lack of adapted vegetable soybean cultivars that are suitable as a vegetable crop. Cultivars currently grown in a small production system are of Japanese origin, and are less adapted to U.S. environmental conditions. Second, there are no efficient ways to harvest and shell vegetable soybean pods. The current operation is labor intensive and not economically attractive. Finally, there is a wide knowledge gap in vegetable soybean food processing and utilization.

For adaptation of edamame as a specialty crop, it is imperative to identify vegetable soybean cultivars that possess desirable agronomic and architectural traits for machine harvest. The objectives of this study were to: 1) determine the efficiency of mechanical harvest for immature vegetable soybean pods and 2) identify vegetable soybean cultivars that are suitable to mechanical harvesting.

MATERIALS AND METHODS

Four potential cultivars, 'Kahala', 'Kanrich', 'Owens', and 'Asmara' from maturity groups (MGs) III, IV, V, and VI, respectively, were planted in four-row plots, in a randomized complete block design (RCBD) with three replications on Abell sandy loam (aquatic Hapridults, fine loamy mixed, thermic), at Randolph Research Farm of Virginia State University, Petersburg, Va during the 2002, 2003, and 2004 growing seasons. Each four-row plot was 60 m x 3 m long, with a spacing of 75 cm between rows and a seeding rate of 23 seeds m⁻¹. Conventional tillage practices were used, and fertilizer was applied following soil test recommendations. Trifluralin herbicide (Treflan HFB, manufactured by DOW, Agro Sciences, LLC, Indianapolis, Ind) was pre plant incorporated into the soil at the recommended rate of 0.56 kg a.i/ha to control weeds.

Harvest and Data Collection

Each cultivar was harvested mechanically with a common bean picker (Pixall BH 100, OXBO, Clear Lake, WI) when plants reached an immature bean stage (R6-R7, Fehr et al., 1971) and expanded to fill 80 to 90 % of the pod width. At the time of mechanical harvest, whole plants from a 1.5 m x 3.0 m section were harvested and placed in a plastic bag and brought immediately to the laboratory where pods were removed by hand, weighed and presented as green pod yield (kg ha⁻¹). One-hundred pods were taken at random and weighed and presented as g 100⁻¹ pods. Ten pods taken at random from the harvested plots were measured (length, width, and thickness) as described by Frank and Fehr (1981) and were presented in cm. Plant height, from ten randomly selected plants were measured in cm.

Experimental Design and Data Analysis.

Data from each year were analyzed separately as a randomized complete block by the Statistical Analysis System Package (SAS, 2001). The homogeneity of error variances were tested before data were combined over years. Cultivars and method of harvest were considered as fixed effects and years as random effects. Year effect was tested for significance using replication within year [rep (y)] as the error term, cultivar effect was tested using the cultivar x year interaction (CYI) as the error term and CYI was tested using the pooled error term. Means were separated via the least significant difference (LSD) procedure at the 5% probability level as described by Steel and Torrie (1980).

RESULTS AND DISCUSSION

The growing conditions during this study varied from year to year. In general, there was sufficient moisture needed for productive plant growth in 2002, 2003 and 2004 growing seasons (Table 1). However, in the 2002 growing season, there was severe drought and higher temperatures during the early pod filling stage.

The combined mean squares analyses for agronomic parameters are presented in Tables 2 and 3. There were significant differences ($P < 0.01$) among years for green pod yield, plant height, one - hundred pod weight, pod length, and pod width. The cultivar and cultivar x year interaction (CYI) effects were significant ($P < 0.01$) for all traits except pod thickness. The significant CYIs suggested the performance of the

TABLE 1. Mean of maximum temperature, minimum temperature, and rainfall for 2002, 2003, and 2004 growing seasons.

Month	Mean Maximum Temp. (C ⁰)			Mean Minimum Temp. (C ⁰)			Mean Rainfall (cm)		
	2002	2003	2004	2002	2003	2004	2002	2003	2004
May	27.2	24.1	27.7	14.6	12.7	16.7	7.29	14.94	10.87
June	33.4	28.4	28.7	16.0	17.0	18.4	6.22	14.86	18.21
July	34.7	30.5	31.0	21.8	20.4	21.1	5.89	14.45	16.99
August	34.0	31.3	28.8	23.6	21.1	19.1	12.07	18.24	24.31
September	29.1	26.5	26.8	20.2	16.2	16.3	4.9	33.27	21.97

TABLE 2. Mean square analysis of variance of green pod yield and plant height of four vegetable soybean cultivars.

Source of variation	df	Green pod yield	Plant height
Year (Y)	2	280131983.5**	19601.7**
Rep[Y]	6	466185.4	40.45
Method (METH)	1	548863994.1	29.90
METH*Y	2	121056135.7**	117.99*
REP(Y)*METH	12	792200.9	27.66
Cultivar (C)	3	14528587.7**	6302.91**
C x Y	6	17792263.0**	468.50**
C x METH	3	21969072.8**	69.13
C x Y x METH	6	4900778.3**	21.29
Pooled error	30	2156898.4	44.86

*, ** Significantly different at the 0.05 and 0.01 probability levels, respectively.

cultivars was not consistent from one growing season to another, and multiple-year testing is required. Among the traits studied, green pod yield and pod width had significant cultivar x method, and cultivar x year x method interactions.

The overall genotypic green pod yield mean was 8831 kg ha⁻¹ and ranged from 7559 kg ha⁻¹ for Kanrich to 9651 kg ha⁻¹ for Owens. None of the cultivars tested produced significantly higher mean green pod yield than the overall green pod mean (Table 4).

The overall plant height mean for the cultivars was 75 cm. Owens had the shortest, while Kahala and Kanrich had the tallest mean plant heights. These two cultivars,

TABLE 3. Mean square analysis of variance of hundred pod weight, pod length, pod width and pod thickness.

Source of variation	df	Hundred Pod weight	Pod length	Pod width	Pod thickness
Year (Y)	2	4490.51**	120.01**	2.86**	21.46
Rep[Y]	6	73.47	5.39	0.18	19.88
Method (METH)	1	333.68	0.13	0.20	26.28
METH*Y	2	230.93	0.13	0.20	26.28
REP(Y)*METH	12	71.81	2.94	0.12	20.28
Cultivar (C)	3	6888.94**	319.50**	16.08**	38.69
C x Y	6	1705.05**	51.83**	1.24**	39.44
C x METH	3	58.68	0.50	0.23**	21.58
C x Y x METH	6	44.88	0.50	0.23**	21.58
Pooled error	30	44.18	2.23	0.04	22.38

TABLE 4. Mean of four vegetable soybean cultivars averaged over three growing seasons, three replications, and two harvesting methods.

Cultivars	Green pod yield (kg ha ⁻¹)	Plant height (cm)	Hundred Pod weight (g)	Pod length (cm)	Pod width (cm)
Kahala	9177	81	97	4.3	0.90
Kanrich	7559	98	127	4.9	1.14
Owens	9651	55	144	5.3	1.06
Asmara	8938	67	128	4.9	1.06
Means	8831	75	124	4.9	1.00
LSD (0.05)	831	4	4	0.1	0.01
CV %	17	9	5	3	2

Kahala and Kanrich also had the lowest hundred pod weight and pod length means. While Asmara and Owens had the highest hundred pod weight and pod length means.

There was also significant cultivar x year interaction. The overall green pod yield mean in the 2003 growing season was higher than both the 2002 and 2004 growing seasons (Table 5). Kahala produced higher green pod yield than the overall means of 2002 and 2004 growing seasons. While Owens produced higher green pod yield than the overall green pod yield means of 2003 and 2004. Kahala and Kanrich were the cultivars that had consistently taller plant height in all three growing seasons. Owens

TABLE 5. Mean of green pod yield, plant height, hundred pod weight, pod length, and pod width of four vegetable soybean cultivars for each three growing seasons (2002, 2003, and 2004).

Cultivar	Green pod yield (kg ha ⁻¹)			Plant height (cm)			Hundred pod weight (g)			Pod length (cm)			Pod width (cm)		
	2002	2003	2004	2002	2003	2004	2002	2003	2004	2002	2003	2004	2002	2003	2004
Kahala	7710	11038	8782	54	95	96	120	91	80	4.3	4.5	4.2	0.89	0.95	0.91
Kanrich	5343	12034	5300	57	106	133	143	132	106	5.3	4.8	4.8	1.20	1.10	1.13
Owens	4721	13627	10607	29	68	69	159	130	143	5.4	5.0	5.6	1.10	0.99	1.10
Asmara	5853	13647	7314	34	79	88	135	101	147	5.5	4.5	4.8	1.10	0.99	1.10
Mean	5907	12586	8001	43	87	96	139	114	114	5.1	4.7	4.8	1.11	1.01	1.01

consistently had lower mean plant height than the overall means of each of the three growing seasons, and also had a higher hundred pod weight than the overall mean of each growing season.

Hand and mechanical harvesting was initiated at the immature green pod stage, when pods were still green and the seeds filled 80-85% of the pod cavity. A significant difference for green pod yield was observed between the manual and mechanical methods of harvesting. The cultivars harvested by hand had green pod yield overall mean of 11592 kg ha⁻¹, while the mechanical harvested cultivars had 6070 kg ha⁻¹. There was a significant cultivar x method interaction. This interaction result suggested that method of harvest was not consistent in harvesting one cultivar from another. Comparing the two methods of harvest, the yield reductions of the cultivars when harvested mechanically were 61, 62, 43, and 26 % for cultivars Kahala, Kanrich, Asmara, and Owens, respectively (Figure 1). In manual harvesting all small pods with a single bean were included in the weight, while in mechanical harvest the small and light pods were blown away along with the leaves and broken stems at the time of harvesting. The two cultivars that seemed to best fit to mechanical harvesting were Owens and Asmara with mean plant heights of 55 and 66 cm, respectively, and Kahala and Kanrich had mean plant heights of 81 and 98 cm, respectively. In this study, a plant height in the range of 55 to 66 cm appeared to be ideal for mechanical harvesting. Cultivars with higher plant height means than Owens and Asmara tended to lose more pods during mechanical harvesting and tended to intertwine with the picker shaft and leave more pods on the plants.

Virginia farmers face severe challenges in today's competitive agriculture situation. Demand for tobacco, that has provided a steady income from farm families throughout mid-Atlantic and Southern states, has fallen off due to successful efforts to reduce smoking. The federal tobacco quota system has been eliminated in recent years through a government buyout. The net result has been a reduction in the amount of tobacco grown and the number of farms growing tobacco. Farmers must now compete on a world market price. This has caused many small farms to no longer produce tobacco. The economic problem is more pronounced among farmers relaying primarily on tobacco as a cash crop. Throughout the Mid-Atlantic and Southern states, tobacco acreage has been on a downward trend for decades, and production has plummeted over the past eight years because of several factors including declining U.S. smoking rates, increased competitive pressure on large cigarette makers and, most significantly, an exodus of buyers to foreign markets such as Brazil and Africa for cheaper tobacco leaf. "In 1997, Virginia farmers made about \$191 million in cash receipts from 53,000 acres of tobacco. By year 2004, tobacco production had dropped to about 30,000 acres" (Blackwell, 2005).

Utilization of mechanical harvesting and identification of cultivars adapted to mechanical harvesting will help Virginia farmers adopt vegetable soybean as an alternative crop production. Farmers already growing soybeans will notice the agronomic practices of vegetable soybeans are similar to grain-type production systems. Therefore, farmers will quickly realize economic benefits from growing vegetable soybean. Soybeans are popular among farmers who practice crop rotation due to their capability to improve soil quality. Vegetable soybeans have a higher profit

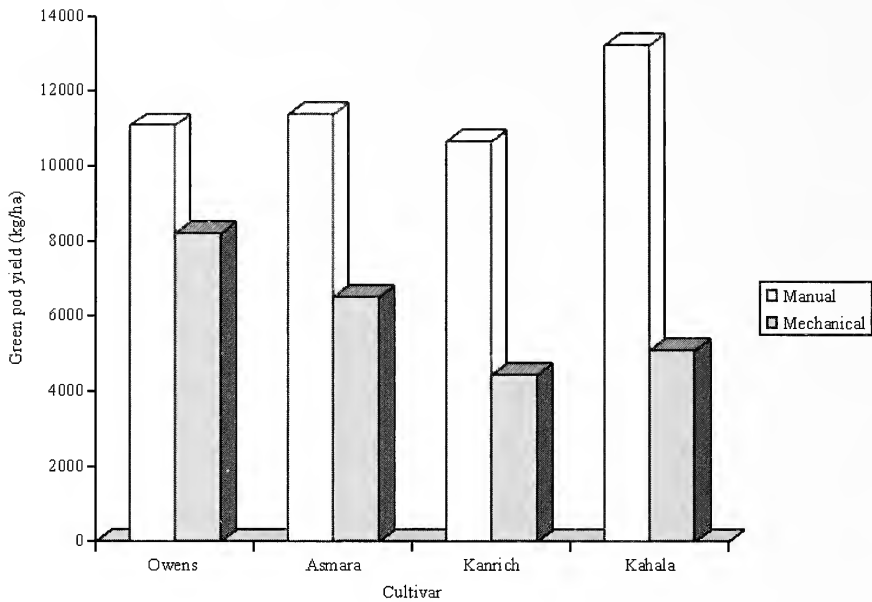


Figure 1. Frequency distribution of green pod yield of vegetable soybean cultivars harvested manually and mechanically.

margin than grain-type soybeans. Karlen et al. (2004) reported that food grade soybean grown organically returned \$1150 to \$1250 ha⁻¹ compared to \$235 for conventional soybean growing in 2 years rotation with corn (*Zea mays* L.).

Although, the United States produces more soybeans than all other soybean producing countries combined it can not meet the growing internal demand of vegetable soybean. At least 70% of the green soybean consumed in the U.S. are imported to meet the market for Asian specialty food products and the increasing number of health conscious individuals. There are around 261,000 Asians in Virginia (U.S. Census Bureau, 2003) alone and they are looking for this specialty soybean. Vegetable soybean is currently gaining popularity with organic growers who target niche commodities for specialty markets and upscale restaurants. Therefore, there is an upward trend for quality soybean cultivars in this niche market. Virginia farmers will require superior cultivars with high nutritional quality to meet this challenge in the near future.

CONCLUSION

Significant difference was observed for green pod yield among hand and mechanical methods of harvest. Comparing hand and mechanical harvest, the yield

reductions of the cultivars when harvested mechanically were 61, 62, 43, and 26 % for cultivars Kahala, Kanrich, Asmara, and Owens, respectively. However, the pods harvested mechanically were cleaner and required no further cleaning as compared to hand harvested pods. The two cultivars that seemed to best fit to mechanical harvesting were Owens and Asmara with mean plant heights of 55 and 66 cm, respectively, and Kahala and Kanrich had mean plant heights of 81 and 98 cm, respectively. This study suggested a plant height in the range of 55 to 66 cm appeared to be suitable for mechanical harvesting. This study further provides valuable information to soybean breeders and producers. First, soybean breeders could include in their breeding programs the development of cultivars with architectural traits that are suitable to mechanical harvest, and second the producers will be able to select before planting cultivars with appropriate plant height for mechanical harvest. Educating the consumers with preparation, cooking, and consumption methods, and developing better flavor and quality varieties are very important for a dramatic increase in demand. This demand, along with the ability to plant cultivars that harvest well mechanically will accelerate vegetable soybean production in Southeast of U.S.

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Correlation of Eastern Wild Turkey Poult:hen Ratios with Population Indices to Detect Reproductive Density Dependence

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ABSTRACT

Knowledge of how density affects population growth is important for the harvest management of wild turkey. Unfortunately, available time-series are often too short for statistical detection of density dependence. The correlation between wild turkey recruitment and population size was assessed using data from 7 state wildlife agencies, circumventing the problem of short time-series by using multiple datasets. Correlation coefficients were calculated between surveyed poult:hen ratios and harvest-based population indices for 31 geographic or harvest management regions. Estimated correlation coefficients were tested for homogeneity to determine if an average correlation could be calculated. Correlation coefficients for the 29 regions ranged from -0.82 to 0.70. A Q-test for homogeneity indicated that correlation coefficients were similar enough to warrant averaging [$Q=25.45$, $df = 28$, $P = 0.603$]. The weighted average correlation coefficient (\pm standard error) was $\bar{r} = -0.30 \pm 0.45$. Population size accounted for little of the variation associated with production ($r^2 = 0.09$). Graphical analysis indicated that a negative correlation between poult:hen ratios and population size tended to occur when the range of population sizes was large. Density dependence appears to have little effect on production. Density-independent models should have better success modeling wild turkey production, while density-dependent effects may have stronger influence on survival or immigration at low population sizes.

Key words: correlation, density dependence, harvest, *Meleagris gallopavo silvestris*, meta-analysis, wild turkey

INTRODUCTION

Evidence that density dependence, the functional relationship between population growth rate and population density, acts on eastern wild turkey (*Meleagris gallopavo silvestris*) populations has increased over the past 30 years (Glidden and Austin, 1975; Healy and Powell, 2001; Turchin, 2003: 398; McGhee, 2006). High growth rates have been reported for reintroduced populations (Little and Varland, 1981; Healy and

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Powell, 2001), while some researchers have attributed low recruitment rates in established populations to the effect of reaching carrying capacity (Glidden and Austin, 1975; Vander Haegan et al., 1988; Miller et al., 1998). Examinations of harvest indices in New York have indicated that wild turkey population growth decreases curvilinearly for population densities of 0-20% of carrying capacity (Porter et al., 1990). McGhee and Berkson's (2007) analysis of harvest time-series from 11 states also indicated a curvilinear decrease in growth rate as populations increased. While observational evidence suggests density-dependent effects on wild turkey population growth, to be useful in harvest management, the mechanisms (i.e., productivity or survival) by which they operate need to be determined.

Population growth in a given region is determined by the rates of births, deaths, immigration and emigration in the population (Pulliam 1988), and density must act on one or a combination of these factors to change the population growth rate under a density-dependent system. It has been assumed that both density-dependent and density-independent factors operate in conjunction to determine annual population growth in harvested species (Bayliss, 1989; McCullough, 1990; Aanes et al., 2002; Guthery, 2002). Detecting density-dependent mechanisms in an environmentally stochastic system typically requires labor and cost-intensive experiments, especially if multiple vital rates must be examined (Armstrong et al., 2005; Hixon and Jones, 2005). However, if researchers can use existing data to explore which vital rates are likely candidates for detecting density-dependent effects, much time and expense may be saved. For example, poult:hen ratios are often collected by state wildlife agencies as indices to recruitment or population size (Healy and Powell, 2000), and may provide an opportunity to examine the linear association between population density and poult production. Poult:hen ratios represent the combined effects of numerous, difficult to estimate reproductive parameters, such as nest rate, nest success, hen success, clutch size and hatching rate (Vangilder 1992). Since poult:hen ratios represent a large portion of the reproductive parameters in a wild turkey population, and are easier for state agencies to obtain, they make a good candidate variable to test the hypothesis that production is density-dependent. If density dependence acts only weakly on production, further research should explore other vital rates more closely. Conversely, if density dependence appears to strongly affect production, further research should focus on specific reproductive mechanisms (e.g., nest rate, hen success, poult survival).

Unfortunately, available time-series are often too short for statistical detection of density dependence (Wolda and Dennis, 1993), and the power of statistical tests are reduced by demographic, environmental and measurement error (McCullough, 1990). These sources of error are expected to be high for indices, increasing the uncertainty in, and possibly biasing parameter estimates (Walters, 1985; Anderson, 2001). Under these limitations, one would not expect any single time-series to produce reliable results. However, if multiple indices are examined for a common parameter, the consequent increase in spatial data may allow consistent patterns to emerge. In essence, statistical power is improved by increasing the number of populations examined, instead of the length of the time-series for a single population, to determine the common parameter among populations (Myers, 2000).

Meta-analysis quantitatively combines information across multiple studies to test a particular hypothesis (Hedges and Olkin, 1985). Independent datasets are the units

of comparison for which summary statistics are calculated and from which inferences are drawn. Meta-analysis techniques have been used successfully with harvest and production indices for sockeye salmon, *Oncorhynchus nerka* (Myers et al., 1997), northern bobwhite quail, *Colinus virginianus* (Williams et al., 2003), ring-necked pheasant, *Phasianus colchicus* (Williams et al., 2003) and eastern cottontail rabbits, *Sylvilagus floridanus* (Williams et al., 2003), and multiple species of marine demersal fish (Myers and Cadigan, 1993). It was assumed that wild turkey harvest indices served as an adequate index to population change for a given management region, requiring the further assumption that harvest of gobblers was proportional to gobbler population size, and that the population sex ratio was constant. Lint et al. (1995) found that this assumption held for wild turkey populations on the Tallahala Wildlife Management Area in Mississippi.

The purpose of this study was to investigate, using meta-analysis, whether wild turkey density affects reproduction. It was hypothesized that a negative linear association existed between population density and poult production. If so, a standard population index, annual spring harvest, should correlate with observed poult:hen ratios (production index) for multiple populations.

METHODS

Harvest and brood data were acquired from seven state wildlife agencies (MD:1996-2001, MS:1995-2002, NC:1988-2001, NJ:1988-2002, NY:1996-2001, RI:1993-2001, VA:1990-1999). Harvest data took five forms: the number of spring gobblers harvested per year (NC, NJ, MD), spring gobblers harvested per km² of forest (VA), spring gobblers harvested per hunter effort (NY, RI), hunter sample surveys (NY, MS, VA), and gobblers heard per 100 hours (survey of hunters in VA). These harvest-based indices were used to track population change over time, assuming a proportional relationship between the indices and true population change for the participating management regions. Datasets were checked for consistent spring harvest regulations and hunter effort, since changes in these would shift or alter the proportional relationship between harvest indices and true density or abundance, potentially invalidating the analysis. Spring season length and bag limits for MD, NC, NY, NJ and VA remained relatively unchanged over the period examined, although issued permits increased in NJ over the time period examined. Participation in spring hunting increased in RI over the period examined, and, in 1998, MS implemented a requirement for harvested gobblers to possess beards ≥ 6 inches. It was assumed that hunter/effort indices incorporated regulation changes such that effort accounted for hunter behavior (MS, NJ, RI).

Brood data took the form of poult:hen ratios for all hens observed, with the exception of RI, where only brood hens were observed. Kurzejeski and Vangilder (1992) state that poult:hen ratios provide a reliable index to annual reproduction. State agencies collect brood survey data during summer over differing months using conservation officers, district biologists, or citizen volunteers. In most cases, brood surveys are conducted during the routine fieldwork by staff, making standardization across samples difficult. This, in addition to the variable effort by volunteers makes direct comparison of poult:hen ratios between states or management regions impossible (Healy and Powell, 2000). This problem is addressed by comparing correlation

coefficients, a standardized measure of the relationship between poult:hen ratios and harvest-based population indices, rather than comparing the raw data (Hedges and Olkin, 1985).

The data were divided into geographic or management regions, producing a total of 29 management units, each comprised of a time-series of poult:hen ratios and some combination of harvest-based population indices. Regions were based on pre-existing management areas or groups of counties conforming roughly to Level III ecoregions as designated by the Environmental Protection Agency (Omernik, 1987). It was assumed that wild turkey habitat remained unchanged over the periods examined for each region (max time-series length = 14 yrs), and that regions were large enough for immigration and emigration to be equal. In some states, management regions changed in area over time. Since this might bias the analysis these regions were not used.

For comparison across populations, estimates of effect size should be dimensionless (Myers, 1997). In this case, the effect size is the slope of the relationship between poult:hen ratios and population density as measured by harvest indices. The correlation coefficient is a dimensionless parameter measuring the degree of association between two variables, and equates to a standardized regression slope (Zar, 1999). This makes it useful for comparing the association of these two variables across populations (Myers, 1997). Since the indices contain unknown amounts of measurement error, it is better to require as few assumptions about the statistical nature of the data as possible. By using the correlation coefficient, a linear relationship is assumed between the compared variables, with observations of both drawn independently of each other (Zar, 1999). For all the states examined, poult:hen ratios and harvest data were collected independently.

Density-dependent effects are more likely to be detected when a wide range of population densities are included in a dataset. To examine the effect that the range of population sizes available exerted on correlations, a ratio of the maximum index value to the minimum index value was calculated for each regional time-series (I_{\max}/I_{\min}). Regional datasets containing a wide range of population index values (and presumably, population densities) had high values of I_{\max}/I_{\min} , while those containing a narrower range of values had lower values of I_{\max}/I_{\min} . A population with an I_{\max}/I_{\min} near 1 would be nearly constant over the time-series with little change in population density.

Correlation coefficients were calculated between poult:hen ratios and population indices by region. When states used more than one index, an average correlation was calculated for each region. Estimated correlation coefficients across regions were tested for homogeneity via a Q-test to determine the appropriateness of calculating an average correlation (Hedges and Olkin, 1985). This test compares each z-transformed correlation coefficient to the weighted average coefficient. Weights were calculated based on the amount of information contributed (I_{\max}/I_{\min}). The weighted z-score was then converted back to a correlation. The standard error of the weighted mean correlation assuming the correlation between indices and poult:hen ratio is fixed across populations is $1/(N-3k)$ where N is the total number of data points across k studies. However, it's more likely that the true correlation varies between populations because habitats are likely to differ, changing the relationship between density and production. In this case the estimated standard error of the true correlation ($\sigma(P)$) may be calculated according to a random effects model, which assumes that the correlation for

any one population is drawn from a distribution (Hedges and Olkin, 1985).

$$\hat{\sigma}(P) = \sqrt{s^2(\hat{p}) - \frac{1}{k} \sum_{i=1}^k (\hat{p}_i^2 - r_i^2)} \quad (1)$$

where \hat{p}_i is an unbiased estimate of the correlation for the i th population when sample sizes are small, $s^2(\hat{p})$ is the sample variance of the population correlation, and r_i is the sample correlation coefficient for the i th population (Hedges and Olkin, 1985).

RESULTS

Correlation coefficients ranged widely for the 29 regions examined (-0.82–0.70: Table 1). The number of years contributed by each region ranged from 6–14 ($\bar{x} = 8.0$, $sd = 2.8$). The Q-test for homogeneity indicated that correlation coefficients were similar enough to warrant averaging [$Q = 25.45$, $df = 28$, $P = 0.603$]. The weighted average correlation across regions was $\bar{r} (\pm SE) = -0.30 \pm 0.45$. Population indices accounted for little of the variation associated with production ($r^2 = 0.09$). For those populations with >1 index, (NY, VA), we assessed the effect on \bar{r} of using only a single index instead of averaging the correlation of both indices. The mean correlation changed little when only single indices were used (range: -0.29–-0.30). Among single regions, only the NJ Coastal Plain demonstrated a significant negative correlation between poult:hen ratio and harvest index ($Z_{0.05(1)} = -2.84$, $P = 0.002$), however, other regions approached significance (NC Coast: $Z_{0.05(1)} = -1.49$, $P = 0.068$; NC Piedmont: $Z_{0.05(1)} = -1.31$, $P = 0.100$; NJ Piedmont: $Z_{0.05(1)} = -1.51$, $P = 0.066$). A graph of regional correlation coefficients against population range (I_{\max}/I_{\min}) shows that those regions with a wider range in population fluctuations tended to have negative correlations between poult:hen ratios and harvest index magnitude (Fig. 1). Those populations with less variation in population fluctuations (low I_{\max}/I_{\min}) showed no relationship between poult:hen ratios and harvest index magnitude. We calculated a post-hoc correlation for those 8 regions having the greatest range of densities ($I_{\max}/I_{\min} > 4$, a natural break in the data: NC, NJ, RI). The correlation for the reduced dataset was stronger, but still statistically insignificant, $\bar{r} (\pm SE) = -0.39 \pm 0.40$.

DISCUSSION

This analysis indicates a biologically insignificant negative relationship between reproduction and population size, explaining only 9% of the variation in poult:hen ratios. This implies that density-dependent factors have little effect on annual production, such that density-independent factors, such as rainfall and temperature during the nesting and brood seasons, may primarily determine annual production (Beasom and Pattee, 1980; Healy and Nenko, 1985). Those states contributing the most information ($> 4 I_{\max}/I_{\min}$: NC, NJ, RI) were geographically widespread, indicating that these results were generally applicable to the central eastern U.S.

TABLE 1. Average correlations between wild turkey poult:hen ratios and harvest indices from 7 U.S. states, ranging from 1988 to 2002. A weighted average correlation was calculated based on the number of years of data available (n). The magnitude of variation in indexed abundance was calculated by dividing the largest index value by the smallest index value (I_{\max}/I_{\min}) as a measure of the variation in population densities available in a time-series. Large values of I_{\max}/I_{\min} represent a greater variety of population densities.

State	Region	r	SE	n	weight	I_{\max}/I_{\min}^a
MD	Appalachian Plateau	0.17	0.41	9	0.01	1.91
	Blue Ridge	-0.18	0.50	7	0.01	1.62
	Coastal Plain	-0.82	0.41	9	0.04	6.28
	Piedmont	0.19	0.41	9	0.02	2.77
	Ridge and Valley	-0.47	0.41	9	0.01	1.54
MS	Region 1	0.70	0.58	6	0.01	2.04
	Region 2	-0.43	0.58	6	0.01	2.17
	Region 3	0.12	0.58	6	0.01	1.78
	Region 4	0.29	0.58	6	0.01	1.56
	Region 5	-0.36	0.58	6	0.01	1.61
	Region 6	0.63	0.58	6	0.02	2.64
NC	Coastal	-0.42	0.30	14	0.06	8.43
	Piedmont	-0.38	0.30	14	0.06	8.58
	Mountains	-0.33	0.30	14	0.05	7.70
NJ	Coastal Plain	-0.46	0.33	12	0.09	13.37
	NE Highlands	-0.31	0.38	10	0.03	4.40
	Piedmont	-0.27	0.32	13	0.09	13.35
	Pine Barrens	-0.18	0.33	12	0.30	43.87
NY	Region 3	-0.35	0.58	6	0.01	1.83
	Region 4	0.32	0.58	6	0.01	1.38
	Region 5	0.27	0.58	6	0.01	1.92
	Region 6	-0.22	0.58	6	0.01	1.52
	Region 7	0.29	0.58	6	0.01	1.96
	Region 8	0.00	0.58	6	0.01	1.33
	Region 9	0.09	0.58	6	0.01	1.86
RI	RI	0.31	0.41	9	0.03	4.96
VA	Northern	-0.18	0.41	10	0.01	1.77
	SW Mountains	-0.13	0.45	9	0.01	1.76
	Tidewater	-0.18	0.41	10	0.01	1.68

^a I_{\max}/I_{\min} for states with multiple indices (NY, VA) are presented as averages

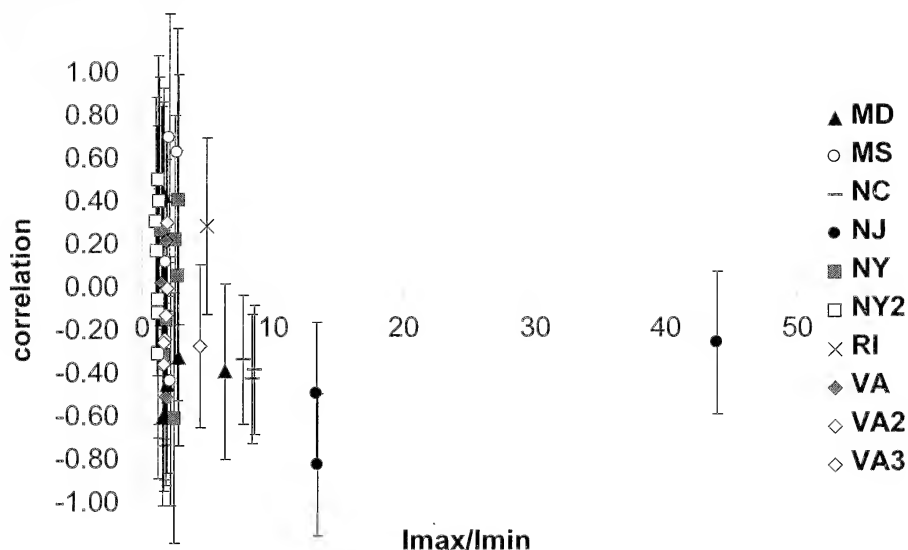


FIGURE 1. Correlations (\pm SE) between wild turkey spring harvest indices and poult:hen ratios for 29 regions in 7 U.S. states, ranging from 1988 to 2002. The x-axis represents the I_{\max}/I_{\min} value for each region, a measure of the population fluctuation within the time-series. Large I_{\max}/I_{\min} values have more information about density changes than low I_{\max}/I_{\min} values. Multiple correlations are listed for states having >1 harvest index. Correlations show high uncertainty and variation between regions, but regions with large I_{\max}/I_{\min} values tend to show a negative correlation between population abundance (harvest indices) and poult:hen ratios. NY refers to reported spring gobblers harvested/effort; NY2 refers to surveyed spring gobblers harvested/effort; VA refers to gobblers heard/100 hours; VA2 refers to surveyed spring gobblers harvested/effort; VA3 refers to spring gobblers harvested/forest km².

Although few studies have attempted to test for density dependence in wild turkey time-series, other bird species have shown much stronger relationships between population density and production. Indices of northeastern U.S. mallard, *Anas platyrhynchos*, population change have been shown to explain 20-36% of the variation in recruitment indices (Sheaffer, 1998). For an experimentally manipulated central European population of collared flycatchers, *Ficedula albicollis*, density explained 59% of the variation in breeding success (Torok and Toth, 1988). Similar associations with population abundance have been shown with partridge chick mortality, *Perdix perdix* (Blank et al., 1967); song sparrow fledgling success, *Melospiza melodia* (Arcese and Smith, 1988); and great tit juvenile winter mortality, *Parus major* (McCleery and Perrins, 1985).

Post-hoc analysis of the most informative datasets showed a slightly stronger correlation, implying that current data may be inadequate to test this hypothesis, even in a meta-analysis framework. However, for the region with the widest fluctuations in population abundance (NJ pine barrens), and therefore, potentially the most informative, harvest indices explained little of the variation in poult:hen ratios ($r^2 = 6\%$). Other studies have indicated that growth rates for wild turkey populations decreased most

dramatically at small population densities relative to carrying capacity, so the detection of density dependence is unlikely unless a wide range of possible population sizes are examined, so that they include periods when populations experience low abundance (Porter et al., 1990; McGhee and Berkson, 2007). Nevertheless, as these data increase, or as newly introduced populations become established, there remains the possibility that density dependence may be detected.

Poult:hen ratios represent the integration of a set of reproductive parameters such as nest rate, nest success, & hen success (Vangilder 1992). While it's possible any or all of these factors may experience some density-dependent effects, ultimately, the size of the brood produced by these factors appears to be overshadowed by density-independent effects. Future modeling attempts should continue to focus on density-independent factors to model production for the eastern wild turkey. Indeed, previous work has indicated that environmental conditions can be important determinants to wild turkey production (Mosby, 1967; Sæther et al., 2004). For example, spring rainfall and temperature explained 58% of the variation 20-day nest survival, and 21% of the variation in 25-day poult survival for a wild turkey population in New York (Robert and Porter, 1998a,b).

A caveat to our results is that the indices used in this analysis are subject to unknown amounts of measurement error, which may have confounded detection of a relationship. Regional correlations varied widely, presumably because the short time-series, lack of population change, inherent environmental variation and measurement error reduced the reliability of any single correlation (Anderson, 2001). Limited data or data with large amounts of measurement error will introduce uncertainty or bias about inferences or parameter estimates (Walters and Ludwig, 1981). Well-designed long-term studies specifically focused on the relationship between reproduction and population density may yield stronger results. However, harvest and brood survey data currently represent the only information available approaching the necessary length and variety of population densities to address the question. Based on this current data, it appears that density is biologically unimportant to poult production.

Poult:hen indices are subject to multiple biases that can potentially affect inferences (Healy and Powell, 2000). These include observation bias by cooperating volunteers and field staff, and the formation of multiple broods as summer progresses (Leopold 1944). As the probability of observing a poult varies by habitat and age, poults may be undercounted, resulting in a consistent negative bias independent of population abundance. As counts are usually taken from roadsides, differences between roadside and non-roadside broods will also consistently affect poult:hen ratios. While consistent biases independent of population abundance would not affect the inferences made here, poult:hen ratios would artificially decrease if sampling times shifted to later summer with the formation of multiple broods. Such a change seems not to have occurred in the data sets examined, as they are either conducted over the entire summer or consistently during specific months.

While the results of this paper imply primarily density-independent production, other vital rates may be more strongly influenced by density-dependent effects. It is likely that both act on population growth at varying degrees at different abundances. Indications of density-dependent effects on presumably r-selected species have increased, producing useful management implications (Higgins et al., 1997; Aanes et al., 2002). Research in harvest management for the wild turkey should attempt to include

both density-dependent and independent influences in harvest models. The effects of strong density dependence at low population abundances may act to offset over harvests or poor production years. In addition, such research would provide a more complete knowledge of the population dynamics at various densities, necessarily providing managers with greater ability for sustainable management of an important game species.

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